

noted that two species (*P. glauca* and *P. hypoleuca*) were distinct in having heteropolar and bilateral “boat-shaped” (see also WALKER & DOYLE, 1975, p. 697) pollen grains, with psilate (smooth) surfaces, and with “... medium-sized perforations in the tectum.” WALKER maintains these latter two species in the genus despite their distinct pollen characters.

At a more informal level, SINCLAIR (1955), treating only those members occurring in Peninsular Malaysia, indicated that this complement of the genus could be subdivided into a number of morphologically distinct groups. Although he designated ten such groups (p. 280), he did not explicitly define any characters by which they could be delimited, nor did he give any of them formal status. SINCLAIR made no mention of pollen in his treatment, and presumably pollen characters were not implicitly used in his classification. However, he placed *P. glauca* and *P. hypoleuca* in his Group 1 of section *Monoon*; these were the two species WALKER noted as differing in pollen characters from the other species of *Polyalthia* examined. Thus, two authors independently identified a close morphological relationship between these two species based on two different sets of characters.

SINCLAIR's Group 1 forms the basis for what ROGSTAD (1986, 1989) has called the *P. hypoleuca* complex, although the latter circumscription of the group included substantial modifications. Further, ROGSTAD described a suite of seven characters that are shared by all members of the complex, this suite apparently being absent in other taxa of the family. Although SINCLAIR did not indicate the morphological characters used to delimit his Group 1, it is likely that he was implicitly using some of these seven characters in recognizing the group. In addition, one of the seven characters is the “boat-shaped” pollen first noted by WALKER (1971a).

The suite of seven characters ROGSTAD used to delimit the *Polyalthia hypoleuca* complex includes : 1) a rare type of papillae on the undersides of the leaves ; 2) leaf veins that are very small in diameter, with tertiary veins nearly indistinguishable from secondary veins ; 3) very numerous secondary veins that are closely spaced ; 4) bark that is fundamentally white ; and 5) ruminations of the seeds that are needle-like. Finally, the pollen is a type that is rare in the family, as is discussed below, and provides two more characters that distinguish the complex.

Earlier systems of classification (e.g., see HOOKER & THOMSON, 1872; SINCLAIR, 1955; FRIES, 1959; and HUTCHINSON, 1964) have used the characters of imbricate versus valvate petal aestivation to distinguish Tribe *Uvarieae* from Tribe *Unoneae*, respectively. ROGSTAD (1986, 1989) has shown, however, that both types of aestivation are found among members of the *P. hypoleuca* complex. While the fact that all members of the complex possess the suite of seven characters noted above is compelling evidence for recognizing them as closely related species, the occurrence of the two different petal aestivation character states in the group makes its placement within the family problematic. This situation has necessitated a broader examination of the family in order to determine the most likely candidates for inclusion in, or as the sister taxon to, the *P. hypoleuca* complex. To this end, we examined all taxa with pollen having a shape even remotely similar to that found within the *P. hypoleuca* complex for the possession of other characters used in its delimitation. In the analyses below, our search for groups related to the complex is divided into two categories : 1) an examination of species within the genus which will prove most useful if current classifications prove correct ; and 2) a survey of taxa outside the genus to shed light on possible related groups given that the need for a revised taxonomic placement of the complex is demonstrated.

We initially take the stance that monosulcate, boat-shaped pollen morphology is a

uniquely derived character state (a synapomorphy) indicative of common ancestry of one or several groups within the *Annonaceae*, rather than a character state that was present in one or a number of ancestral lineages of the family and that has undergone alteration in all but a few closely and/or only remotely related taxa of the family (a symplesiomorphy). In the discussion section we also explore the possibility that the latter is the case, and it will be seen that this has little effect on our conclusions. In addition, comparisons of the distributions of other character states between the *P. hypoleuca* complex and all other taxa known to possess monosulcate, boat-shaped pollen are made to support the conclusion that the complex is a monophyletic group, or at the least, a group including all and only the members of a larger monophyletic taxon that occur in a restricted geographic region. First, however, our findings concerning pollen characters within the complex will be presented.

METHODS

Information concerning pollen character states for species not included in the *P. hypoleuca* complex was derived from the literature (see references) except where noted. Voucher and herbarium specimens examined for this study are listed in Appendix 1. Non-pollen, morphological character states were determined directly from these specimens when possible; in a few cases designations were obtained from the literature. Pollen sample vouchers were determined according to ROGSTAD (1986, 1989).

Fresh flowers in all stages of development were collected from *P. discolor*, *P. hypoleuca*, *P. glauca*, and *P. multinervis*. Only late-to-mature phase fresh flowers of *P. sumatrana*, and flowers from herbarium specimens of *P. ovalifolia*, were available. Fresh flowers were fixed in 95% ethanol : 5% glacial acetic acid for 24 hours and then stored in 80% ethanol. Field observations of flowering were made at the sites given in ROGSTAD (1986), and fresh pollen observations were made using dissecting microscopes available at Pasoh Forest Reserve (Malaysia) and at April River (Papua New Guinea; courtesy Kennicott Mining Operations), and with compound microscopes made available courtesy of the staffs at Kuala Pilah Hospital (Negri Sembilan, Malaysia), at the Forest Research Institute (Kepong, Selangor, Malaysia), and thanks to Dr. V. SANDS (University Malaya, Kuala Lumpur). Photographs of pollen of *Asimina triloba* pollen were made using a Wild M-8 dissecting microscope fitted with a Nikon FE camera.

Pollen germination experiments were performed using solutions of sucrose serially diluted with sterilized (previously boiled) water to different concentrations (20% sucrose weight : volume, 10%, 5%, 2.5%, 1.25%, and pure water). A copious amount of pollen (from that had just dehisced) was added to a drop or two of each sucrose dilution on microscope slides, and the drops were then covered with cover slips. These slides were placed in sealable plastic bags along with water saturated tissue to prevent desiccation of the sucrose solutions.

For SEM analysis, pollen grains were acetolysed at 80°C, and examined with a Jeol Scanning Electron Microscope (Laboratoire de Géologie, Muséum National d'Histoire Naturelle, Paris). We are grateful to M. WAHA (Institut Für Botanik, Universität Wien) for TEM examinations of the pollen of members of the complex (methods given in WAHA, 1985).

RESULTS

Observations of the floral biology of five members of the *P. hypoleuca* complex have been reported previously (ROGSTAD, 1986). In all of these species, pollen is available to pollinators for only one to two hours before the flowers shatter (abscission of the petals and stamens). At least for *P. discolor*, *P. glauca*, *P. hypoleuca*, and *P. multinervis*, pollen shape is not an artifact of solvent or drying effects as proposed by GOTTSBERGER & SILBERBAUER-GOTTSBERGER (1984) since pollen grains collected at anther dehiscence are clearly heteropolar and boat-shaped

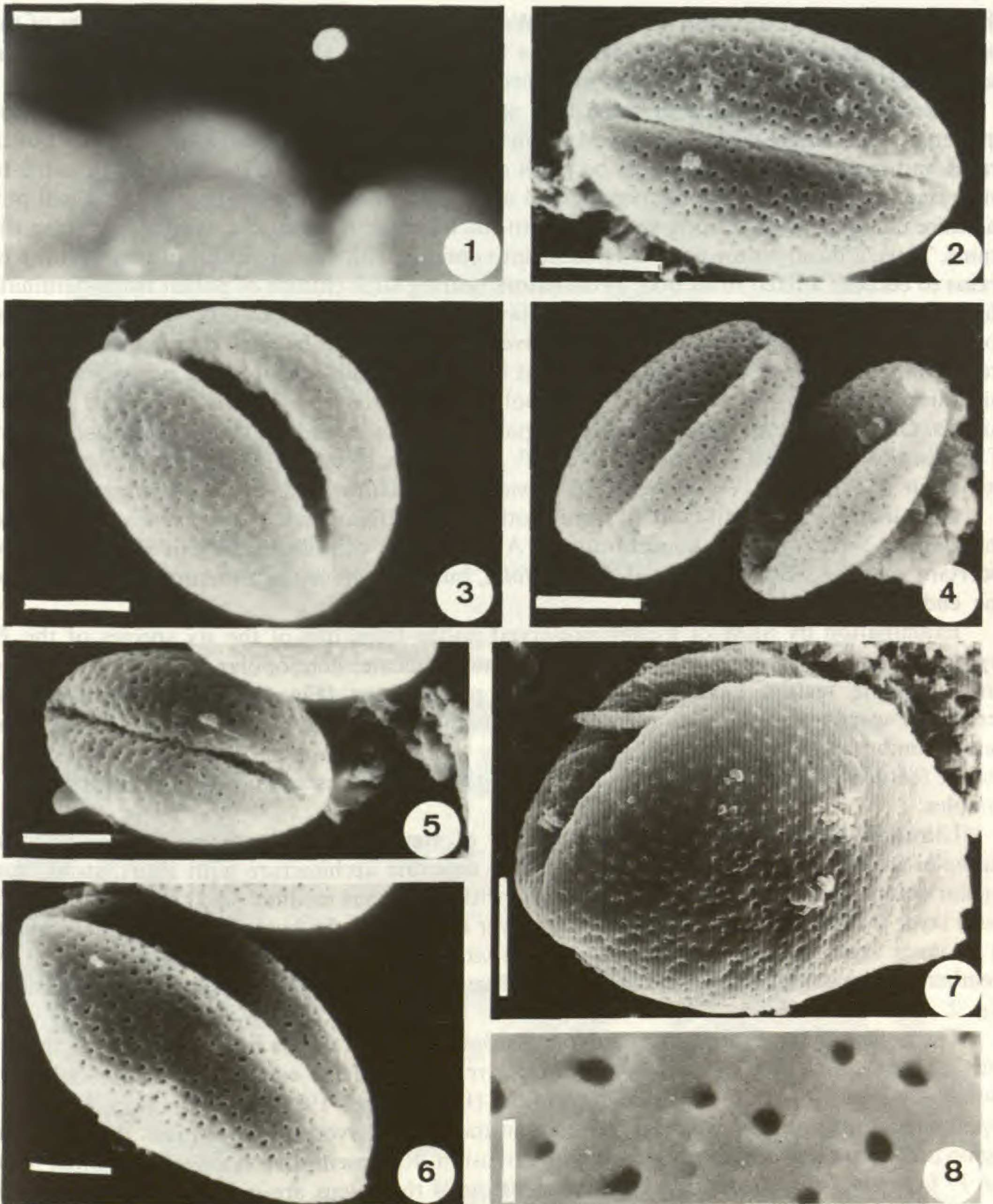


Fig. 1. — 1, pollen tetrad from fresh flower of *Asimina triloba* suspended by sticky "threads" that form the pollen exudate when tetrads are pulled lowly apart (the tetrad is overexposed to ensure that the thread would be visible); scale bar = 0.3 mm; 2-7 : pollen grains of the different species of the *Polyalthia hypoleuca* complex, SEM, scale bar = 10 μ m; 2, *P. discolor*; 3, *P. glauca*; 4, *P. hypoleuca*; 5, *P. multinervis*; 6, *P. sumatrana*; 7, *P. ovalifolia*; 8, magnified view of the exine surface of the pollen of *P. hypoleuca*, SEM; scale bar = 1 μ m.

when viewed with a compound microscope. We assume this to be the case for all species of the *Annonaceae* for which this pollen shape has been reported, although we acknowledge that more observations of fresh material are needed.

The fresh pollen of each of these four species was covered with a sticky exudate (the "pollenkitt" of HESSE, 1981?) that acts as an adhesive both for the agglomeration of pollen grains and for attachment of grains or grain clusters to pollinators. It is usually possible to touch one grain with a dissecting needle, and upon withdrawing the needle, the grain will pull an entire clump of pollen along with it due to the adhesive force of the exudate covering the grains. Thus, a floral visitor need only come into contact with one grain for an entire clump of grains to become affixed to its body. Pollinators bearing such clumps of pollen from staminate phase flowers of each of these four species have been observed (ROGSTAD, pers. obs.). When pollen is fresh, the adhesive quality of the covering exudate can be demonstrated by pulling a grain gently apart from the clump to which it is attached, the exudate then being drawn into thin threads. In Fig. 1, 1 a tetrad of fresh pollen from *Asimina triloba* is suspended by such threads. One of us (ROGSTAD) has observed pollen exudate threads in staminate-phase flowers of *P. discolor*, *P. glauca*, *P. hypoleuca*, and *P. multinervis*, all of the *P. hypoleuca* complex, as well as in *P. lateriflora*, *P. sclerophylla*, *Monodora myristica*, and an *Oncodostigma* species.

Germinations of fresh pollen from both *P. longifolia* and *P. hypoleuca* were most abundant at 5-10% sucrose concentrations. A clear point of pollen tube exit was difficult to ascertain with the globose pollen of *P. longifolia*, but in *P. glauca* germination was usually to one end of the heteropolar grain.

Examination by SEM of freshly preserved pollen from five of the six species of the *P. hypoleuca* complex demonstrates that all have monosulcate, heteropolar, boat-shaped pollen with a psilate tectum having medium sized perforations (Fig. 1, 2-8). Pollen from an herbarium specimen of the sixth member of the complex, *P. ovalifolia*, examined with SEM is clearly similar to that of the other members (Fig. 1, 7). A more highly magnified view of the surface features of a grain from *P. hypoleuca* (Fig. 1, 8) is representative of all members of the complex.

Ultrathin sections of pollen from species of the *P. hypoleuca* complex (see selected examples in Fig. 2) reveal that the grains have an exine architecture with short, stout, and regular columellae, and a tectum that is psilate with numerous medium sized perforations. The basal layer is bipartite with 1) a thick outer layer connecting the bases of the columellae, and 2) an inner layer of discontinuous, lamellar foliations (LUGARDON & LE THOMAS, 1974). All members of the complex have the pollen wall characters depicted for representative species in Fig. 2.

The pollen of the *P. hypoleuca* complex is similar to that of the majority of other species with monosulcate pollen in that there is a clear reduction of the exine at the sulcus, which is usually covered by a thin apertural membrane (LE THOMAS, 1981, p. 320; 1988). In the *P. hypoleuca* complex, the alveolar (or tubular) intine becomes very thick towards the apertural region and increases considerably during its extrusion. Representative examples of pollen from the *P. hypoleuca* complex transected in the region of the sulcus are given in Fig. 2, 1 and 3.

We conclude from the TEM and SEM analyses that these pollen features appear to be uniform throughout the *P. hypoleuca* complex. As will be seen below, some of these character states are relatively rare in the family (WALKER, 1971a; LE THOMAS, 1981). Thus, they are correlated with, and can be added to, the other five relatively rare character states noted

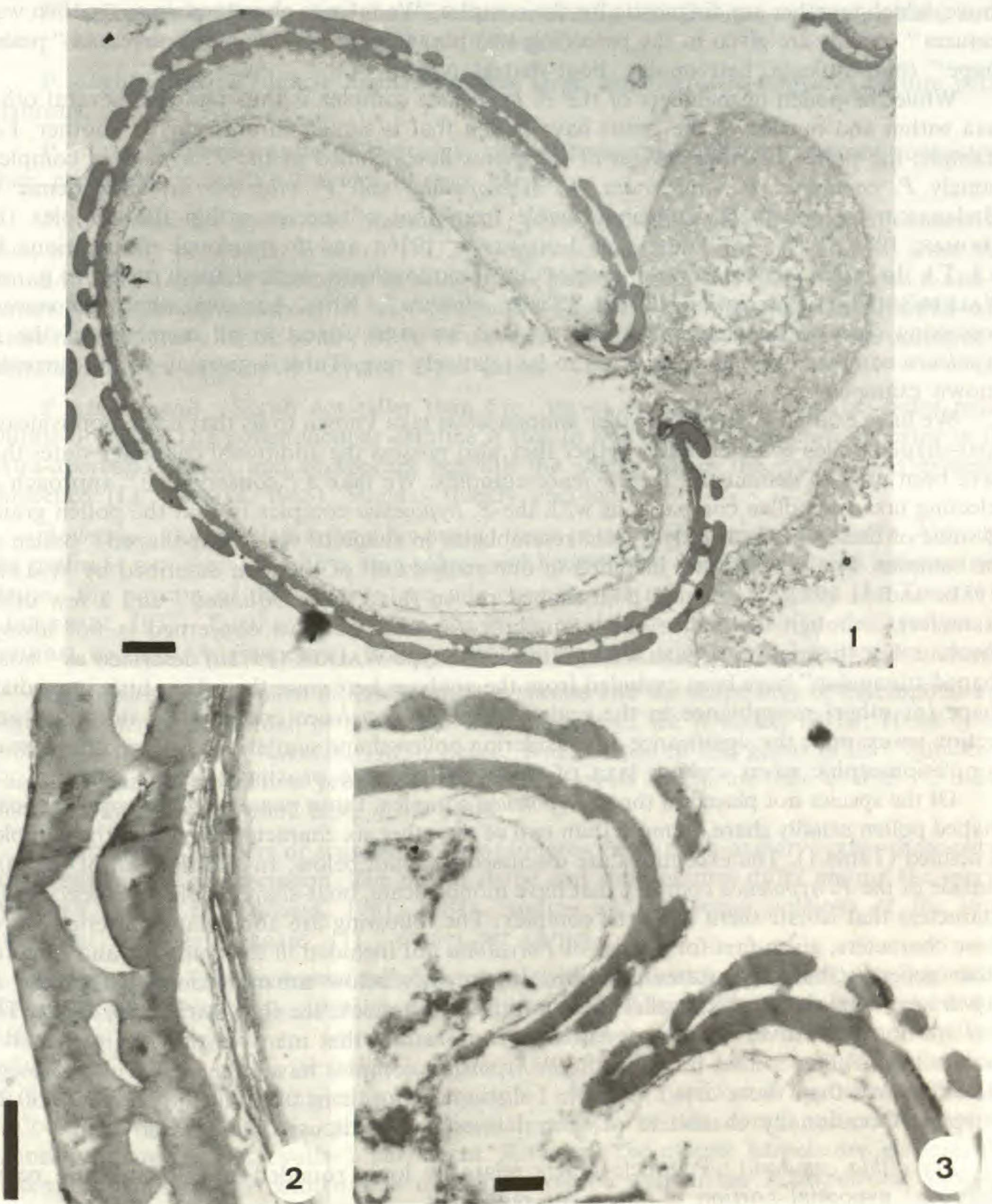


Fig. 2. — TEM ultrasections of selected species of the *Polyalthia hypoleuca* complex showing the pollen wall structure from examples representative for all the species of the complex : 1, *P. sumatrana*, the intine extruded; scale bar = $0.2\ \mu\text{m}$; 2, *P. glauca*, extra-apertural region; scale bar = $0.5\ \mu\text{m}$; 3, *P. hypoleuca*, in the sulcus region; scale bar = $0.5\ \mu\text{m}$.

above, which together are diagnostic for the complex. We refer to character six as “pollen wall features” (details are given in the preceding two paragraphs) and character seven as “pollen shape” (monosulcate, heteropolar, boat-shaped pollen).

While the pollen of members of the *P. hypoleuca* complex is thus uniform, several other taxa within and outside of the genus have pollen that is similar in one way or another. For example, the pollen of other species of the genus not included in the *P. hypoleuca* complex, namely *P. capuronii*, *P. emarginata*, *P. heteropetala*, and *P. oligosperma*, all endemic to Madagascar, is practically indistinguishable from that of species within the complex (LE THOMAS, 1981, 1988; LE THOMAS & LUGARDON, 1976*a* and *b*; personal observations by A.L.T.). In other genera several species have monosulcate, boat-shaped pollen, e.g., see WALKER'S (1971) description of his “Tribe *Malmea*”. Note, however, that *Annonaceae* possessing both pollen character states six and seven as found in all members of the *P. hypoleuca* complex must be considered to be relatively rare (Table 1 gives all of the currently known examples).

We have examined all of the other annonaceous taxa known to us that have monosulcate, boat-shaped pollen to determine whether they also possess the additional character states that have been used to delimit the *P. hypoleuca* complex. We take a “conservative” approach in selecting taxa for pollen comparisons with the *P. hypoleuca* complex in that the pollen grains of some of these taxa bear only a faint resemblance in shape to the “boat-shaped” pollen of the complex. For example, we included in our analyses all of the taxa described by WALKER (1971*a* and *b*; 1972*b*) as having boat-shaped pollen (his “Tribe *Malmea*” and a few other examples), although the pollen shape similarity among the taxa concerned is not always absolute. For the most part, taxa with grains of the type WALKER (1971*a*) described as “boat-shaped-triangular” have been excluded from the analyses here since these bear little immediate shape (or other) resemblance to the grains of the *P. hypoleuca* complex. In the discussion section we examine the significance of considering pollen shape similarity as synapomorphic or symplesiomorphic when seeking taxa of close phylogenetic proximity to the complex.

Of the species not placed in the *P. hypoleuca* complex, those possessing heteropolar, boat-shaped pollen usually share no more than two of the other six characters by which the complex is defined (Table 1). The exceptions are discussed in detail below. In addition, all of the taxa outside of the *P. hypoleuca* complex that have monosulcate, boat-shaped pollen possess certain characters that isolate them from the complex. The following are abbreviated descriptions of these characters, given first for species of *Polyalthia* not included in the complex, and then for other genera. Characters states described in the lists below are not found within the *P. hypoleuca* complex (for the parallel states within the complex, see ROGSTAD, 1986, 1989). The lists are not exhaustive, but are presented to demonstrate that many of the taxa with pollen morphology similar to that found in the *P. hypoleuca* complex have other major morphological differences than those listed in Table 1 distinguishing them from all the members of the complex. Occasionally characters of special interest are discussed in greater detail.

Polyalthia capuronii : Peduncle bracts relatively long, rounded apically; mature petals glabrous; gynoecial portion of the torus pubescent.

P. emarginata : Leaves apically emarginate with raised midrib adaxially; leaf domatia present where the secondary veins meet the midrib on the abaxial leaf surface; mature petals glabrous; gynoecial portion of the torus pubescent.

P. heteropetala : Petals more than 6, often or usually with 3 outer, subovate petals, and 9 linear inner petals that are longer than the outer.

P. oligosperma : Peduncle bracts relatively large and narrowly obovate; mature petals glabrous.

P. oliveri : Flowers andromonoecious; petals remaining connivent; stamen connectives thin, produced conically; 2 ovules in each carpel.

P. suaveolens : Flowers andromonoecious; petals remain connivent; stamen connectives thin, irregularly produced. WALKER (1972*b*) suggested that the pollen is different from that found in the *P. hypoleuca* complex in being inaperturate and on this basis he placed it and *P. oliveri* (= *Greenwayodendron*) in his "Subfamily *Fusaea*", an interpretation followed with some reservation by HESSE et al. (1985). In contrast, LE THOMAS (1981) found the pollen of *P. suaveolens* to be aperturate. Ovules 2 per carpel.

P. stuhlmannii : Shrub not taller than 5 m; leaves relatively chartaceous; outer petals elliptic-obovate. The pollen lacunar exintine is two to five times thicker than the exine in the extra-apertural region and disappears beneath the sulcus where the endintine is evidently thickened (LE THOMAS, 1988). Stigmas thickly obconic.

Ambavia : Outer petals triangular-ovate; inner petals fleshy, keeled abaxially. Although the pollen is monosulcate with a long sulcus and heteropolar, it is unique in its asymmetrical shape : the portion of the grain on the side opposite the sulcus is irregular (LE THOMAS & LUGARDON, 1977). Further, the pollen has intine that is much thinner at the aperture (in contrast to most Angiosperms). Stamen connectives with trichomes; 2 ovules per carpel.

Anaxagorea : The pollen differs among the species and the shape may be heteropolar and slightly bilateral, ellipsoidal, or suboblate to globose (e.g., see WALKER, 1971*a*; HESSE et al., 1985; LE THOMAS & LUGARDON, 1985); hence, WALKER placed this genus in his "Subfamily *Fusaea*". Stamen connectives produced; the mature carpels are clavate follicles with 1-2 black, smooth, shining seeds that taper to a point.

Artabotrys : Climbers or scandent shrubs; inflorescences extra-axillary; inner three petals connivent basally at abscission. The pollen shape and wall features differ among the species (WALKER, 1971; LE THOMAS, 1981, 1988). Andro- and gynoecial portions of the torus pubescent; stigmas elongate; (1) 2 ovules per carpel.

Bocageopsis : Leaf epidermal cells have angular idioblasts with amorphous (silica?) contents (SETTEN & KOEK-NOORMAN, 1986); leaf primary vein raised adaxially; petals triangular-ovate. Pollen surface irregular to verrucate (WALKER, 1971*a*) with exine structure irregularly columellate (WAHA, 1985); the pollen interpreted as operculate by LE THOMAS & THANIKAIMONI (1987) but with operculum entirely ectexinous, i.e. with a thickened apertural membrane (GUINET & LE THOMAS, in press); gynoecial portion of the torus pubescent; stamen connectives constricted; ovules 2 per carpel. Although the mature carpels are globose, the placentation is basal, a combination of characters not seen in the *P. hypoleuca* complex. SETTEN & KOEK-NOORMAN (1986) report papillate trichomes on abaxial leaf surfaces for some members of this genus, and although we have been unable to confirm the occurrence of trichomes in *Bocageopsis* similar to the papillate of the *P. hypoleuca* complex, we have taken a conservative position in Table 1.

Cleistochlamys : Leaf apices rounded or emarginate; flowers sessile; sepals wholly connate, the calyx being ruptured as the floral bud develops. The pollen surface rugose-verrucate (WALKER, 1971a) and the pollen wall not fully columellar (LE THOMAS, 1987). Styles cylindrically elongated.

Cleistopholis : A specimen of *C. glauca* (Leeuwenberg 6467) has small leaf papillae somewhat similar to those found in the *P. hypoleuca* complex. The papillae of *C. glauca* differ in that they are not present on all leaves of the collection and even vary on one leaf; they also appear to interconnect irregularly. In contrast, the papillae described for the *P. hypoleuca* complex are present on all leaves, are very uniform over the entire surface of each leaf, and never interconnect. Sepals imbricate; outer petals much longer than inner; stamen thecae lateral. The pollen surface is smooth and microperforate, and the infratectal layer of the exine is granular (LE THOMAS, 1987). Stigma discoid; ovules 2 per carpel.

Cremastosperma : Leaf primary vein raised adaxially; some species cauliflorous; sepals imbricate. Pollen with columellate exine and thickened exintine lacunar at the aperture; WAHA (1986) kept this genus, based on pollen characters, in "Tribe *Malmea*" sensu WALKER (1971a). Ovule pendulous and attached near or slightly below the apex of the loculus.

Enantia : Bark and wood yellow or sulphur colored; leaves with compound stellate trichomes; inflorescences extra-axillary; only three petals per flower. LE THOMAS (1981) describes the exine architecture as being very similar to that of *P. capuronii*, which, as noted above, is virtually indistinguishable from that of the *P. hypoleuca* complex. Intine distribution was later used to interpret this pollen as pontoperculate (LE THOMAS & THANIKAIMONI, 1987). Gynoecial portion of the torus pubescent.

Ephedranthus : Leaf epidermal cells have rhombic crystals and angular idioblasts with amorphous (silica?) contents (SETTEN & KOEK-NOORMAN, 1986); leaf primary vein raised adaxially. SETTEN & KOEK-NOORMAN (1986) indicated that papillate trichomes on abaxial leaf surfaces are found in this genus, and although we have been unable to confirm the similarity between such trichomes and the papillae of the *P. hypoleuca* complex, we take a conservative stance in Table 1. Flowers unisexual; large bracts enclose the floral buds. WAHA (1985) concluded that, of the four genera of WALKER's "Tribe *Malmea*" examined by TEM, pollen from *Ephedranthus* is the closest in tectum architecture to that of *P. capuronii*. In this paper we demonstrate that this architecture is also very similar to that of the *P. hypoleuca* complex. Gynoecial portion of torus pubescent; smooth testa of seeds with fine striations perpendicular to a circumferential seed groove (seeds are very similar to those characterizing the *P. lateriflora* — *P. sclerophylla* cluster of species; ROGSTAD, 1986, 1989; SINCLAIR's Group 6, 1955).

Kingstonia : Pedicel bract present just below the calyx; sepals imbricate, connate at the base; stamens ca. 9-12; one carpel per flower; stigma peltate; ovules several in two rows; and mature pericarp thick.

Lettowianthus : Sepals elongate, with rounded apices. WALKER (1972b) and LE THOMAS (1981) provide evidence that the pollen of this genus is quite different from that found in the *P. hypoleuca* complex. Based on pollen characters, WALKER (1971a) and HESSE et al. (1985) place *Lettowianthus* in WALKER's "Subfamily *Fusaea*". Styles very elongate, clavate, prismatic, not radiating; ovules 2 per carpel.

Malmea : Leaf epidermal cells containing rhombic crystals and angular idioblasts with amorphous (silica?) contents (SETTEN & KOEK-NOORMAN, 1986); leaf primary vein raised adaxially; inflorescences extra-axillary; sepals overlap; petals rounded-oval shaped. Pollen exine reticulate, with a granular infratectal layer (WAHA, 1985). Gynoecial portion of the torus pubescent and deeply concave.

Meiocarpidium : Leaves have peltate scales; inflorescences leaf-opposed. HESSE et al. (1985) and LE THOMAS & LUGARDON (1985) suggested that the pollen is very similar to that of *Anaxagorea*. Numerous ovules per carpel; seeds asymmetrical, rounded to one side.

Monocarpia : Inflorescences extra-axillary; stigma large and discoid; numerous seeds in very large, sessile, solitary mature carpels.

Onychopetalum : Leaf epidermal cells have angular idioblasts with amorphous (silica?) contents (SETTEN & KOEK-NOORMAN, 1986); leaf primary vein raised adaxially. The leaves of some species have a fine indumentum below, but this is more irregularly distributed than found in the *P. hypoleuca* complex, and the trichomes are very short but filamentous (and see SETTEN & KOEK-NOORMAN, 1986). However, we have taken a conservative stance in Table 1. Sepal margins sinuate, imbricate; petals ovate; inner petals with an inflexed apex or apical appendage; stamen connectives elongated; carpels 1 (2) per flower; style cylindrical; four or more ovules per carpel.

Oxandra : Leaf epidermal cells containing angular idioblasts with amorphous (silica?) contents (SETTEN & KOEK-NOORMAN, 1986); leaf primary vein raised adaxially. Leaf venation is sometimes fine in this genus, but never matches that found in the *P. hypoleuca* complex. Sepals imbricate; petals often white; stamens 6-25; anthers ending in a lanceolate ligule and with separate loculi. WAHA (1986) retained *Oxandra* in "Tribe *Malmea*" sensu WALKER (1971a), but proposed two distinct evolutionary lines of the tribe on the basis of intine distribution, which is here reminiscent of that of *Polyalthia stuhlmanii*. Mature carpels with very short stipes.

Piptostigma : Outer petals similar to the sepals in size, the inner petals much longer; andro- and gynoecial portions of the torus pubescent. Pollen with a granular exine structure (VAN CAMPO & LUGARDON, 1973); included, based on pollen features, in the "Subfamily *Fusaea*" sensu WALKER (1971a). Stigmas united; numerous ovules in each carpel.

Polyceratocarpus : Flowers andromonoecious. From pollen features, LE THOMAS (1981) placed this genus near *Meiocarpidium*. Ovules numerous in each carpel; mature seeds asymmetrical, flattened on one side.

Pseudephedranthus : Leaf epidermal cells containing rhombic crystals (SETTEN & KOEK-NOORMAN, 1986); leaf primary vein raised adaxially; sepals reniform; torus conic-acute; stamen connective thin, elongated ventrally.

Pseudoxandra : Leaf epidermal cells bear angular idioblasts with amorphous (silica?) contents (SETTEN & KOEK-NOORMAN, 1986); leaf primary vein raised adaxially; sepals imbricate; petals ovate. The pollen grains are in tetrads. WALKER (1971a) claims that the only example of anasulcate pollen in the family is found in this genus. LE THOMAS (1981, p. 318) disagrees indicating that the furrows of all the *Annonaceae* with monosulcate pollen are distal. Ultrastructural analyses confirm the latter interpretation for pollen of *Pseudoxandra* lacking

proximally reduced exine (LE THOMAS et al., 1986). *Pseudoxandra polyphleba* pollen is verrucate (LE THOMAS et al., 1986) relative to the more psilate pollen of the *Polyalthia hypoleuca* complex. Carpels prism-shaped; ovule and seed pendulous; mature carpels with very short stipes.

Ruizodendron : Leaf epidermal cells containing rhombic crystals (SETTEN & KOEK-NOORMAN, 1986); leaf primary vein raised adaxially. The leaves may have minute abaxial trichomes, but these are irregularly interconnected in a web-like fashion (and see SETTEN & KOEK-NOORMAN, 1986). However, we have taken a conservative position on this character in Table 1. Sepals imbricate; mature carpels depressed-globose with lateral placentation.

Unonopsis : Leaf epidermal cells containing angular idioblasts with amorphous (silica?) contents (SETTEN & KOEK-NOORMAN, 1986); leaf primary vein raised adaxially; long, perenniating inflorescences may be present; petals broadly ovate, concave, and relatively thick. Pollen exine granular or somewhat irregularly columellate; very similar to *Bocageopsis* pollen (WAHA, 1985). Gynoecial portion of the torus pubescent; ovules more than one per carpel in some species.

TABLE 1 : Distribution of diagnostic character states for the *Polyalthia hypoleuca* complex in other Asian species of *Polyalthia*, and in other taxa with sulcate, heteropolar, boat-shaped pollen. See text for a detailed description of the character states. Taxonomic placement of these taxa according to WALKER (1971a) and FRIES (1959) is indicated. + = character similar or the same; - = character different; + - = both states clearly exist in the taxon; (?) = some difficulty in interpretation exists and further investigation needed (e.g., similarity not exact; not clearly present in all members of the taxon; etc.); a conservative approach has been taken in which all such questionable character states have been scored as "+"; N = neotropical; A = African; M = from Madagascar.

CHARACTER :	POLLEN WALL FEATURES ¹	LEAF PAPILLAE	NUMEROUS 2° LEAF VEINS	2° VEINS SMALL DIAMETER	SEED RUMINATION NEDDLES	BARK WHITE	TAXON PLACEMENT ²	
							WALKER	FRIES
TAXON								
All species of the <i>P. hypoleuca</i> complex (Asian)	+	+	+	+	+	+	m	p
Other Asian species of the genus (pollen not sulcate, boat-shaped)	-	-	-	-	- ³	-	m	p
African region								
<i>Polyalthia</i>								
<i>P. capuronii</i> (M)	+	-	-	-	+ (?)	-		
<i>P. emarginata</i> (M)	+	-	-	-	-	-		p
<i>P. heteropetala</i> (M)	+	-	-	-	-	-		
<i>P. oligosperma</i> (M)	+	-	-	-	+	-		p
<i>P. oliveri</i> (AF)	-	-	-	-	+	-		p
<i>P. stuhlmanii</i> (AF)	-	-	-	-	+ (?)	-		
<i>P. suaveolens</i> (AF)	-	-	-	-	+	-	f	p

TABLE 1 (continued).

CHARACTER :	POLLEN WALL FEATURES ¹	LEAF PAPILLAE	NUMEROUS 2° LEAF VEINS	2° VEINS SMALL DIAMETER	SEED RUMINATION NEDDLES	BARK WHITE	TAXON PLACEMENT ²	
							WALKER	FRIES
Other genera								
<i>Ambavia</i> (M)	—	—	—	—	—	—		
<i>Anaxagorea</i> (Asia-N)	—	—	—	—	—	—	f	x
<i>Artabotrys</i> (Asia)	—	—	—	—	—	—	u	ar
<i>Bocageopsis</i> (N)	—	+ (?)	—	—	+	—	m	un
<i>Cleistochlamys</i> (A)	—	—	—	—	—	—	h	h
<i>Cleistopholis</i> (A)	—	—	—	—	—	—		a
<i>Crematosperma</i> (N)	+ (?)	—	—	—	+ —	—	m	a
<i>Enantia</i> (A)	+	—	—	—	+	—	m	ar
<i>Ephedranthus</i> (N)	+ (?)	+ (?)	—	—	—	—	m	a
<i>Kingstonia</i> (Asia)	+ (?)	—	—	—	—	—	u	p
<i>Lettowianthus</i> (A)	—	—	—	—	—	—	f	h
<i>Malmea</i> (N)	—	—	—	—	—	—	m	d
<i>Meiocarpidium</i> (A)	—	—	—	—	—	—	f	de
<i>Monocarpia</i> (Asia)	—	—	—	—	—	—	u	de
<i>Onychopetalum</i> (N)	—	+ (?)	—	—	+ (?)	—	m	un
<i>Oxandra</i> (N)	—	—	—	+ —	+ —	+ —	m	a
<i>Piptostigma</i> (A)	—	—	—	—	+ (?)	—	f	x
<i>Polyceratocarpus</i> (A)	—	—	—	—	+	—	u	un
<i>Pseudephedranthus</i> (N)	—	+ (?)	—	—	—	—	m	
<i>Pseudoxandra</i> (N)	—	—	+ —	+ —	+	+ —	m	a
<i>Ruizodendron</i> (N)	—	+ (?)	—	—	—	—	m	a
<i>Unonopsis</i> (N)	—	—	—	—	+	—	m	un

1. Tectum is psilate with medium sized perforations; exine has short, stout, and regular columellae; the basal layer is bipartite with an outer layer connecting the bases of the columellae, and an inner layer discontinuous, lamellar foliations.

2. Under WALKER: *Annona* Subfamily: h = *Hexalobus* Tribe. *Fusaea* Subfamily: f = a member of this small subfamily. *Malmea* Subfamily: m = *Malmea* Tribe; u = *Uvaria* Tribe.

Under FRIES: Tribe *Unoneae*: ar = *Artabotrys* Groups; de = *Desmos* Group; p = *Polyalthia* Group; un = *Unonopsis* Group; x = *Xylopi* Group. Tribe *Uvarieae*: a = *Asimina* Group; d = *Duguetia* Group; h = *Hexalobus* Group; u = *Uvaria* Group.

3. An exception, *P. suberosa*, is discussed in the text.

Table 1 includes most of the taxa known to possess one or more character states from the suite of seven under consideration. However, a few taxa that lack pollen of the shape characterizing the taxa listed in Table 1 (and hence they are not included in the table) do express one of the other character states of Table 1. One species of *Polyalthia* (*P. suberosa*) has spiniform ruminations but none of the other six characters diagnostic for the complex. Similarly, *Orophea* Blume, *Pseuduvaria* Miquel, *Popowia* Endl., and *Richella* A. Gray, have at least some species with spiniform seed ruminations. All of these taxa lack any of the other characters that unite the species of the *P. hypoleuca* complex, and differ from the complex in additional characters. Thus none of them are strong candidates for inclusion in, or as a possible outgroup to, the complex. It should be noted that KESSLER (1988, p. 11; pers. com.) has suggested a possible relationship of *P. suberosa* with *Orophea*, *Popowia*, and *Pseuduvaria*.

DISCUSSION

We have demonstrated that the pollen of all the species included in the *P. hypoleuca* complex is extremely homogeneous in both shape and pollen wall architecture. Thus these two pollen characters are highly correlated with, and can be added to, the suite of delimiting characters for the complex. If pollen shape is used as an indicator of phylogenetic relationship, several taxa must be further examined as possible candidates either for inclusion in the complex or as the sister group (outgroup) to the *P. hypoleuca* complex. As noted earlier, tribal placement of the complex is problematic, and therefore the search for such taxa has been extended beyond the genus *Polyalthia* and the tribe to which it is usually assigned (Tribe *Unoneae*). The approach here has been to examine all of the taxa known to have a similar pollen shape (although, as noted above, we have taken a "conservative" approach in that many taxa considered have only a very general similarity in pollen shape).

Similar pollen shape shared between two taxa may be due to one (or more) of several causes. Such similarity may be an artifact, although we have argued above that the pollen shape found for all members of the *P. hypoleuca* complex is not due to artifacts of pollen treatment in the sense of GOTTSSBERGER & SILBERBAUER-GOTTSSBERGER (1984). Furthermore, we assume that the similarity of pollen shape within the complex to the pollen of the other taxa discussed here is not such an artifact, unless further evidence to the contrary is forthcoming. The possibility also exists that the same shape has been achieved in different taxa through parallel or convergent evolution. In all of these cases, it is unlikely that comparisons of the *P. hypoleuca* complex with other phylogenetically removed taxa will reveal many other similar character states. Thus, those taxa that share only general pollen shape with, but differ in a great many other characters from, the *P. hypoleuca* complex (e.g., *Anaxagorea*, *Artabotrys*, *Cleistochlamys*, etc.) may share pollen shape similarity as the result of one of the explanations above.

Finally, it is possible that morphological similarity is a result of descent from a common ancestor. The characters used to distinguish the *P. hypoleuca* complex can for the most part be considered as rare in *Annonaceae*. Such characters (or at least some of them) are either derived and the complex can be considered a monophyletic group, or the *P. hypoleuca* complex lineage is cladistically basal to some larger clade of the family and the seven relatively rare character states are all symplesiomorphic states for the clade. The latter seems unlikely.

If similarity of pollen shape between the *P. hypoleuca* complex and another taxon is a trait inherited through a common ancestral lineage, then either 1) the latter taxon diverged before the radiation of the species in the *P. hypoleuca* complex from a common ancestor that had acquired all of the traits by which the complex may be delimited, or 2) the taxon diverged from within the complex. For most of the taxa listed in Table 1, namely those possessing only one or a few of the complex-defining characters, the latter case can be considered to be more unlikely since it assumes the loss of nearly all those characters. Thus, it is most parsimonious to consider any such taxon as having diverged before the evolution of the characters that define the complex. Further, in such a case, the character states not possessed by the earlier diverging taxon lineage but found in all the members of the *P. hypoleuca* complex are then most parsimoniously interpreted as synapomorphies for the lineage leading to the complex,

thereby substantiating the monophyly of the lineage. In other words, once an outgroup is determined for the complex, synapomorphies for the complex can be designated.

However, the clarity of the placement of a taxon relative to the *P. hypoleuca* complex decreases as the number of character states from Table 1 shared between the taxon and the complex increases. For example, with a taxon sharing monosulcate, boat-shaped pollen and all but two of the character states of Table 1 with the *P. hypoleuca* complex, it is more difficult to determine whether that taxon is a sister group to, or a lineage divergent from within, the complex (an example is given in Fig. 3). While it is most parsimonious to exclude such a taxon from the complex, placing it within the complex increases the length of the resulting character change cladogram by only two steps. If only the most parsimonious case is considered, then the two characters not shared become synapomorphies for the complex. If, on other grounds, it is decided that the taxon is a clade within the now paraphyletic *P. hypoleuca* complex, then the two characters not shared by all taxa can be considered as derived in the ancestral lineage to the *P. hypoleuca* complex — taxon clade, but now lost in the taxon.

Given the above observations of characters and the discussion of taxon placement based on the sharing of character states, the taxa under consideration can be examined as candidates for inclusion in, or as the sister group for, the *P. hypoleuca* complex. The best choices are first, those taxa sharing the greatest number of character states diagnostic for the *P. hypoleuca* complex with the complex, and then, taxa that in addition have the greatest number of character states shared with, or that are the least divergent from, other characters of the *P. hypoleuca* complex.

Considering Table 1, from within the genus, the Asian complement of *Polyalthia* not placed within the complex for the most part lacks any of the seven character states in the suite. LE THOMAS (1988) demonstrated that several of these species have disulcate pollen. From the African-Madagascar region, *P. oligosperma*, and possibly *P. capuronii*, both from Madagascar, potentially share the greatest number of characters defining the *P. hypoleuca* complex. Therefore, from within *Polyalthia*, these two species are the best candidates for an outgroup for the complex.

It should be noted that the Asian *P. longifolia*, which SINCLAIR (1955) placed in his Group 1 along with three of the species included here in the *P. hypoleuca* complex, differs from the complex in both pollen shape (although it as a short sulcus) and exine characteristics (LE THOMAS, 1981). ROGSTAD (1986, 1989) also described several other characters by which *P. longifolia* differs from the members of the *P. hypoleuca* complex, and further noted it lacks all of the character states used to define the complex.

Comparisons with other genera shows that, with the exception of pollen shape, the characters diagnostic for the *P. hypoleuca* complex are not of common occurrence in Asian or African representatives of the family, and while not abundant in Neotropical taxa, they are more common in the latter. Further, it is of interest to examine whether or not the 13 genera with heteropolar, boat-shaped pollen that possess one or more of the other six characters defining the *P. hypoleuca* complex (Table 1) have been placed by previous investigators in close phylogenetic relationships with one another. For example, in WALKER's classification (1971a), 11 of these 13 genera were placed in his "Subfamily *Malmea*", "Tribe *Malmea*". Only one genus of this tribe, *Malmea*, lacks all of the six characters. This result indicates the other six characters may in some way be correlated with pollen shape (the major feature uniting WALKER's "Tribe *Malmea*"), and further, the relatively high concentration of these character

states in this tribe may reflect phylogenetic relationships. Examining the treatment of the family by FRIES (1959), seven of the 13 other genera are placed in Tribe *Unoneae* (in four groups), while five are placed in Tribe *Uvarieae* (in one group; one genus is not treated), and thus the distribution of these characters is not so clearly correlated with his classification system.

Concerning the question of which genera are the most likely candidates for inclusion in, or as outgroups to, the *P. hypoleuca* complex, it can be seen from Table 1 that all but two of the 22 genera listed have only one to three of the seven character states diagnostic for the complex. Of the two genera with more, *Oxandra* has four and *Pseudoxandra* has five. Although the expression of these character states is often interspecifically polymorphic in both *Oxandra* and *Pseudoxandra*, their presence in these two genera suggests a possible, relatively close phylogenetic relationship between them and the *P. hypoleuca* complex (assuming, of course, that *Oxandra* and *Pseudoxandra* are both monophyletic groups). An understanding of this relationship is complicated by the fact that, although five of the seven character states used to delimit the *P. hypoleuca* complex are found in *Pseudoxandra*, no one species of the genus has all five. In fact, we have been unable to find a single species of *Pseudoxandra* with more than three of the seven characters states. However, the question of whether the *Pseudoxandra* clade should be placed within the *P. hypoleuca* complex (thus rendering the latter paraphyletic), or treated as its sister group is not affected by this polymorphic character distribution, although, as noted above, the latter alternative is somewhat more parsimonious. The placement of *Oxandra* and *Pseudoxandra* relative to the *P. hypoleuca* complex is examined in Fig. 3.

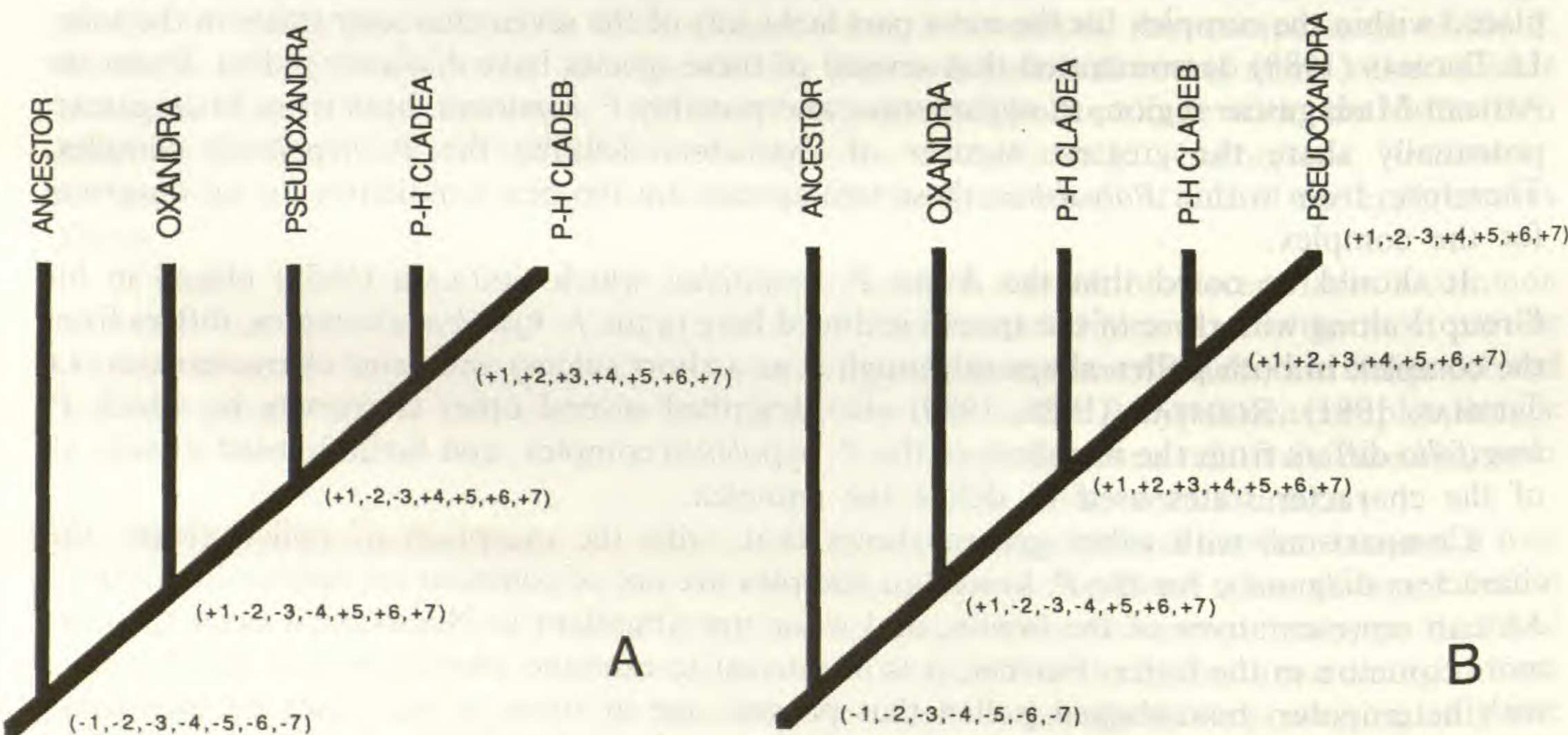


Fig. 3. — Cladograms of two phylogenetic hypotheses for the relationship of the *P. hypoleuca* complex to the best candidate (*Pseudoxandra*) as the sister-taxon to (A), or for inclusion within (B) the complex. Here, the complex has been theoretically divided for illustrative purposes into two clades, P-H Clades A and B. Fig. A is the most parsimonious cladogram for the data set, although B is only two evolutionary steps longer. Sympleisomorphic characters indicated by a $-$, synapomorphic characters indicated by a $+$: $+1$ = pollen heteropolar, boat-shaped; $+2$ = pollen wall features (see text); $+3$ = leaf papillae; $+4$ = numerous 2° leaf veins; $+5$ = 2° veins small diameter; $+6$ = seed rumination needles; $+7$ = white bark. For further explanation, see text.

We conclude that based on the distribution of the seven character states used to diagnose the *P. hypoleuca* complex, *P. oligosperma* and *P. capuronii* from Madagascar are the most likely candidates, from *Polyalthia*, as sister taxa to the complex. When considering the entire family, *Pseudoxandra* (or perhaps the *Pseudoxandra* — *Oxandra* complex of species) are most parsimoniously considered to be the outgroup for the complex. With only slightly less likelihood, *Pseudoxandra* may be considered as a lineage that branched from within the *P. hypoleuca* complex. In the latter case the complex becomes a paraphyletic group. However, as *Pseudoxandra* is Neotropical and the *P. hypoleuca* complex is restricted to Malesia, the complex can be considered at the least to include all and only those members of a larger monophyletic taxon that occur in a restricted geographic region. Some of the implications of such groups are explored in ROGSTAD (1986, 1989).

That the relatively rare character states diagnostic for the *P. hypoleuca* complex find their densest distribution in a group of Neotropical taxa, occur sporadically in taxa of the African region, and are very rare among the Asian taxa (including other Asian species of *Polyalthia*), suggests that the *P. hypoleuca* complex does have closer ancestral ties with some of the Neotropical taxa (or African species including some from *Polyalthia*) than with other Asian taxa. This conclusion holds regardless of whether or not the related taxa are outgroups for, or clades within, the complex. Assuming that long-distance dispersal events are rare, such ties must be ancient, dating to the breakup of Gondwanaland or earlier. Further investigations of characters denoted with question marks in Table 1, and of new characters, are needed to bear out this hypothesis.

Monosulcate, boat-shaped pollen is found throughout the “ranalean complex” and the gymnosperms (e.g., see WALKER, 1976; MULLER, 1970), and using the “woody ranales” as an outgroup, this shape may be considered as a primitive character state within the *Annonaceae*. While this character state thus may be a shared primitive character (symplesiomorphy) in the family, it is correlated with several other relatively rare characters, some or all of which, as noted above, can be considered synapomorphies, and thus the conclusions reached here would not be altered.

LE THOMAS (1981) noted the similarity between the pollen of four species of *Polyalthia* from Madagascar (*P. capuronii*, *P. emarginata*, *P. heteropetala*, and *P. oligosperma*) and two congeners from Malaysia (*P. glauca* and *P. hypoleuca*), using this pattern to support a model of *Annonaceae* spread from West Gondwanaland to Asia via the tectonic drifting of India. Our results here also indicate possible related lineages that have diverged from Gondwanan origins. However, the two Malaysian species are now included in the *P. hypoleuca* complex that has some members in Papua New Guinea, and thus the spread of the lines ancestral to the *P. hypoleuca* complex by more southerly routes cannot be ruled out (RAVEN & AXELROD, 1974; VAN BALGOOY, 1976). Additional information on the phylogeny of the members of the *P. hypoleuca* complex may shed light on this ambiguity.

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APPENDIX

The following herbarium specimens were used to make the morphological observations reported above. Attempts were made to examine flowering and fruiting specimens of at least 10 % of the species of a genus. Often several individuals of a species were examined, and only representative specimens are listed here. Literature information was also used to confirm and supplement these direct observations.

- Anaxagora javanica* Blume var. *tripetala* Corner : Elmer 21131 (A).
A. luzonensis Gray : Ramos BS 13623 (A).
A. petiolata R. E. Fries : A. C. Smith 3192 (MO).
A. phaeocarpa Mart. : Anderson 12139 (MO).
A. rufa Timmerman : Gentry & Tillett 10883 (MO).
A. sylvatica R. E. Fries : Mexia 5053 (MO).
- Artabotrys harmandii* Finet & Gagnep. : Pierre 423 (A).
A. siamensis Miq. : Sargent s.n., 16.10.1903 (MO).
A. suaveolens Bl. : Maxwell 81-206 (MO).
A. trichopetalus Merr. : Elmer 20489 (A).
A. zeylanicus Hooker f. & Thomson : Saldanha 16365; Waas 934 (both A).
- Asimina triloba* (L.) Dunal : Rogstad 843 (MO).
- Bocageopsis canescens* (Spruce) R. E. Fries : Prance et al. 5929, 8792 (both MO).
B. mattogrossensis (R. E. Fries) R. E. Fries : Mass et al. 6242 (MO).
B. multiflora (Mart.) R. E. Fries : Prance et al. 22714; Prance 25798 (both MO); Silva & Rosario 5849 (A).
- Cleistochlamys kirkii* (Benth.) Oliv. : Pereira & Correia 2351; de Carvalho 1045 (both MO).
- Cleistopholis glauca* Pierre ex Engl. & Diels : Louis 12459, 12563; Leeuwenberg 6467 (all MO).
C. patens (Benth.) Engl. & Diels : Darko 732; Louis 7993 (both MO).
C. staudtii Engl. & Diels : Bates 1568 (MO).
- Crematosperma anomalum* R. E. Fries : Correa & Dressler 887, 1060 (both MO); Stern et al. 107 (A).
C. cauliflorum R. E. Fries : Bristan 1341; Lleras et al. 16879; Diaz & Jaramillo 1229 (all MO).
C. gracilipes R. E. Fries : Foster 9560 (MO).
C. macrocarpum Maas : Liesner & Gonzalez 9763 (MO).
C. pedunculatum (Diels) R. E. Fries : Klug 3726 (A).
C. pendulum (R. & P.) R. E. Fries : Vigo 7251 (MO).
- Enantia chlorantha* Oliv. : Bates 1959; Leeuwenberg 7355; Zenker 441 (all MO).
E. polycarpa (DC.) Engl. & Diels : Baldwin, Jr. 10696 (MO).
- Ephedranthus amaxonicus* R. E. Fries : Prance et al. 18787, 11555 (both MO).
E. guianensis R. E. Fries : Gentry et al. 29075 (MO).
E. pisocarpus R. E. Fries : Schatz et al. 732 (MO).
- Kingstonia nervosa* Hooker f. & Thomson : Forest Dept. 4083; Goodenough 1329; S.F.N. 14946 (all SING).
- Lettowianthus stellatus* Diels : Seusei S1027 (MO).
- Malmea depressa* (Baill.) R. E. Fries : Lundell 4852 (MO); Croat 24646 (MO).
M. obovata R. E. Fries : Riedal s.n. (A).

- Meiocarpidium lepidotum* Engl. & Diels : *de Wilde* 1942 A, 2735; *Zenker* 3602 (all MO).
- Monocarpia marginalis* (Scheff.) J. Sinclair : *de Vogel* 4492 (MO).
- Monodora myristica* Dunal : Observations made on a specimen growing at the forest Research Institute, Kepong, Selangor, Malaysia.
- Oncodostigma* sp. : *Rogstad* 920 (A).
- Onychopetalum krukoffii* R. E. Fries : *Krukoff* 5326 (MO).
- O. lanceolatum* R. E. Fries : *Krukoff* 6909 (MO).
- O. lucidum* R. E. Fries : *Krukoff* 8214 (MO).
- Oxandra acuminata* Diels : *Croat* 19729 (MO).
- O. asbeckii* (Pulle) R. E. Fries : *Mori & Boom* 15170 (MO).
- O. eneura* Diels : *Croat* 18738 (MO).
- O. espintana* (Spruce) Baill. : *Gentry, Aronson & Ramirez* 26744 (MO).
- O. lanceolata* (Sw.) Baill. : *Curtiss* 701; *Fuertes* 224; *Proctor* 36333 (all MO).
- O. laurifolia* (Sw.) A. Rich : *Beard* 460, *Duss* 4180 (both MO); *Ekman* 5924 (A).
- O. leucodermis* (Spruce) Warm. : *Liesner* 6983; *Liesner & Clark* 8949 (both MO).
- O. longipetala* R. E. Fries : *Duke* 4850; *Gentry* 3285; *Holdridge* 6213; *Stern et al.* 739 (all MO).
- O. panamensis* R. E. Fries : *Duke* 10257 (MO).
- O. xylopioides* Diels : *Huashikat* 1257 (MO).
- Piptostigma fasciculata* (De Wild.) Boutique : *Toussaint* 2151; *Germain* 2396 (both MO).
- P. glabrescens* Oliv. : *Thomas* 510 (MO).
- P. pilosum* Oliv. : *Thomas* 4726, 4755 (both MO).
- Polyalthia capuronii* Cav. & Keraudren : *Capuron SF* 11795 (P).
- P. emarginata* Diels : *Capuron* 20977-SF (P).
- P. discolor* Diels : *Rogstad* 814, 832 (A).
- P. glauca* (Hassk.) Mueller : *Rogstad* 939, 944, 945, 966 (all A).
- P. heteropetala* Diels : *Ghesquier* 4942 (P).
- P. hypoleuca* Hooker f. & Thomson : *Rogstad* 912, 916, 942 (all A).
- P. lateriflora* (Blume) King : *Rogstad* 931 (A).
- P. longifolia* (Sonnerat) Thwaites : *Rogstad* 960 (A).
- P. multinervis* Diels : *Rogstad* 813, 817-819, 829 (all A).
- P. oligosperma* (Danguy) Diels : *Thouvenot* 62 (P).
- P. oliveri* Engl. & Diels : *Baldwin, Jr.* 10394; *Enti* 1701; *Oldeman* 856 (all MO).
- P. ovalifolia* S. H. Rogstad : *Buwalda* 7797 (A).
- P. sclerophylla* Hooker f. & Thomson : *Rogstad* 930 (A).
- P. stuhlmannii* (Engl.) Verdcourt : *Harris* 3635 (MO).
- P. suaveolens* Engl. & Diels : *Gilbert* 8500; *Leeuwenberg* 5082, 7322 (all MO).
- P. suberosa* (Roxb.) Thwaites : *Rogstad* 844 (MO).
- P. sumatrana* (Miq.) Kurz : *Rogstad* 508, 509, 527 (all A).
- Polyceratocarpus gossweileri* (Exell.) Paiva : *Breyne* 752 (MO).
- P. microtrichus* (Engl. & Diels) Ghesq. & Pellegr. : *Zenker* 478 (MO).
- P. parviflorus* (Bak. f.) Ghesq. : *Bos* 6684; *Jacques-Georges* 16832 (MO).
- Pseudephedranthus fragrans* (R. E. Fries) Aristeguieta : *Maguire et al.* 60189 (MO).
- Pseudoxandra coriacea* R. E. Fries : *Prance, Steward, Ramos & Pinheiro* 11468 (MO).
- P. cuspidata* Maas : *C. C. Berg et al.* 757; *Prance & Sylva* 58673 (both MO).
- P. guianensis* R. E. Fries : *A. C. Smith* 2665 (MO).
- P. lucida* R. E. Fries : *Rimachi* 2310; *Steyermark & Delascio* 129373 (both MO).
- P. polyphleba* (Diels) R. E. Fries : *Croat* 19243 (MO); *Gentry, Vasquez, Andrade, Horna & Stern* 28807 (MO); *Krukoff* 8409 (MO); *Vasquez & Jaramillo* 284 (A).

Ruizodendron ovale (R. & P.) R. E. Fries : *Begazo 61*; *Klug 3798* (both MO).

Unonopsis pittieri Safford : *Contreras 10031*; *Lent 2289* (both MO).

U. floribunda Diels : *Gentry 7452* (MO).

U. panamensis R. E. Fries : *Johnston 1643* (MO).

U. spectabilis Diels : *Maas et al. 6229* (MO).

Uvaria boniana Finet & Gagnep. : *Tsang W. T. 23823* (MO).

U. calamistrata Hance : *Lau 468* (MO).

U. confertiflora Merr. : *Elmer 21081* (A).

U. grandiflora Roxb. : *Rogstad 639* (A).

U. javana Dunal : *Elmer 20857* (MO).

U. littoralis Blume : *de Vogel 3895* (MO).

U. lucida Benth. : *Faden 74/1251*; *Pawek 12051* (both MO).

U. mendesii J. Paiva : *Mendes 629* (MO).

U. muricata Pierre & Engl. : *Gentry & Pilz 32795* (MO).

U. obanensis Bak. f. : *Talbot 1579* (MO).

U. osmantha Diels : *Mendes 673* (MO).

U. ovata A. D.C. : *Jacques-Georges 5850* (MO).

U. poggei Engl. & Diels : *Robyns 4227* (MO).

U. sabrida Oliv. : *Gossweiler 10417* (MO).

U. sofa S. Elliot : *Jacques-Georges 14602* (MO).

New species of *Pseudodissochaeta* Nayar and *Sonerila* Roxb. (*Melastomataceae*) from Indo-China

C. HANSEN

Summary : *Pseudodissochaeta raphioides* from Laos, *Sonerila neodriessenioides* from Vietnam, and *S. tuberosa* from Cambodia are described.

Résumé : Description de *Pseudodissochaeta raphioides* du Laos, *Sonerila neodriessenioides* du Viêt-nam et *S. tuberosa* du Cambodge.

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I. A NEW SPECIES OF *PSEUDODISSOCHAETA* NAYAR FROM LAOS

The new species has been based on two specimens in the Muséum National d'Histoire Naturelle in Paris. It has tentatively been referred to *Pseudodissochaeta*, the only genus to which it shows some affinity. *P. raphioides* agrees with that genus in its narrow short-petiolate leaves arranged in two rows along slender probably arching branches, and otherwise in its slightly dimorphic and slightly unequal anthers with a dorsal spur connected with two ventral lobes (Fig. 1), and in its domed slightly humpy top of the ovary without a crown. Besides, it occurs inside the area of distribution of *Pseudodissochaeta* (NAYAR, 1969).

P. raphioides has been referred to *Pseudodissochaeta* (*Dissochaeteae*) with hesitation because only buds are known, and the relationship may turn out to be wrong if the fruits appear to be capsular. In that case the species belongs in the *Sonerileae* where a new genus will have to be established for it.

P. raphioides differs from the other species in *Pseudodissochaeta* in its secretory cells, present in all vegetative parts and in the hypanthium, sepals, and petals. Externally on a leaf when observed under a lens they look like cells with raphides as in species of *Fordiophyton* and *Phyllagathis* or as the cystoliths on the leaves of the *Acanthaceae*. However in transparency at a higher magnification their content is clearly seen not to be crystals such as raphides, druses or styloids, of which druses (stellate aggregates of crystals) are common in the *Sonerileae*, but looks like an agglomerate of minute grains. Its nature has not been clarified. Their presence, readily observed on the leaf surface, distinguishes *P. raphioides* also from all other species of the *Dissochaeteae* and of the *Sonerileae*, except those species in *Fordiophyton* and *Phyllagathis* with raphides.

P. raphioides differs from the other species of *Pseudodissochaeta* also in its conspicuous indumentum and in the absence of ribs on stem or an interpetiolar ridge.

Four species (*P. assamica*, *P. lanceata*, *P. spirei*, and *P. subsessilis*) have large terminal

thyrses, and in its axillary inflorescence *P. raphioides* resembles only the fifth species, *P. septentrionales*. In both the inflorescence is raceme-like and composed of the central axis with (1-)2-3 nodes on its distal half with opposite one-flowered geniculate "branches", each really being a short true branch ending in a node from which springs a short-pedicelled flower.

Establishing the new genus *Pseudodissochaeta*, NAYAR (1969) seemed to have solved the relationship of a number of species described in various genera and on occasion transferred to others, but apparently alien to all. His genus has since been accepted by various authors (VELDKAMP & NAYAR, 1978; MAXWELL, 1980, 1983; VLIET, 1981), and new synonyms added. Nevertheless CHEN (1984) did not agree and included the genus in *Medinilla*. VLIET's studies of the wood anatomy in the *Melastomataceae* (1981), however, strongly support that *Pseudodissochaeta* should be accepted as a genus of its own, which shares characters with the subtribe *Dissochatinae* rather than with the *Medinillinae*. *P. rosea* (Guill.) Maxw. is capsular fruited and belongs elsewhere.

***Pseudodissochaeta raphioides* C. Hansen, sp. nov.**

Frutex pilis patentibus arcuatis rigidis, paucis vel pluribus cum glandula parva elongata et sparsis tantum in pagina superiore foliorum, cellulis secernentibus albidis numerosis in foliis atque inflorescentibus axillaribus brevibus et paucifloribus.

TYPE : *Poilane 26428*, Haut Laos, province du Haut Mekhong, entre Tafa et B. Houei Soi (holo-, P).

Branched shrub, 1.5-2 m high, with a dark indumentum of minute bent uni-seriate hairs and patent curved 1-2 mm long stout hairs, few to many tipped with a small elongate gland, on all vegetative parts and on hypanthium and sepals, sparse only on leaves above, and with many secretory cells in most parts. Branchlets subquadrangular to terete, dark, internodes 4-8 cm long. Leaves opposite, in two rows, isomorphic and equal in a pair; petiole 0.5-1 cm long; blade narrowly ovate to elliptic, 9-16 × 2.4-4.5 cm, tapering from about middle; base rounded to subcordate, apex long acuminate, margin entire; 3-5-nerved. Inflorescences axillary raceme-like thyrses, 2-4 cm long, with 1-2 nodes below terminal one, all with opposite 1-2 mm long branches ending in a single flower; bracts inconspicuous, subulate, less than 1 mm long, passing into a stout bristle, or reduced to a bristle. Flowers actinomorphic, 4-merous, bisexual, known only in bud. Hypanthium cup-shaped, ca. 4 × 2 mm. Sepals narrowly triangular, ca. 1 mm long. Petals in bud with apical hairs as hypanthium, white (according to label). Stamens 8, subisomorphic, unequal; anthers (in bud) 3 and 3.7 mm long, connective in both with a dorsal spur and two ventral lobes, but largest and slightly different in structure in the larger anthers; pore 1. Ovary 4-locular, about half as long as hypanthium and adnate to it for its whole length, anther pockets half-way to base, crown absent, top of ovary flat, but slightly humpy, glabrous; placentas protruding into locules. Fruit and seeds unknown. — Buds and flowers in June. — Fig. 1.

HABITAT : Clayey shaly fertile soil in forest at 500-600 m altitude.

DISTRIBUTION : Laos (Houa Khong). Annam, the locality given on *d'Alleizette s.n.* is probably wrong.

SPECIMENS STUDIED : *D'Alleizette s.n.*; *Poilane 26428*.